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Differences in the Frequencies of Several Shell Characters in the Clam *Donax variabilis* Around Cape Hatteras, North Carolina

by

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Abstract. Samples of the coquina clam, *Donax variabilis,* were collected from four sites around Cape Hatteras, North Carolina. The extensive polymorphism in these clams was subdivided into variation for five characters: background color, presence or absence of colored umbo, rays, and rings on the exterior of the shell, and presence or absence of interior pigment. For each clam, the shell was measured for length and scored for the five characters. The sites were highly heterogeneous both for shell lengths and for the frequencies of the qualitative characters. Each site presented a unique combination of shell lengths and morph frequencies, and neither mean shell length nor the frequencies of any of the five characters showed a consistent pattern of differences among the five sites. Most probably, *D. variabilis* in the Hatteras region forms disjunct populations that initiate at different times or respond to extremely local environmental conditions or both. Any future studies must examine changes in *Donax* over very short distances, preferably over at least a year's time.

INTRODUCTION

The coquina clam, *Donax variabilis* Say, 1822 (Bivalvia: Donacidae), has long been noted for the great variety of shell colors and markings found within any one of its populations. The polymorphism has been little studied, however, while considerable attention has been paid to the ecology and behavior of this organism (for an extensive bibliography see NELSON, 1985). Clams of the genus *Donax* possess an ability—to live intertidally on sandy, wave swept beaches—that is so unusual that much attention has been given to the behavioral adaptations that allow this genus to follow the tide in and out, remaining in the wash zone (TURNER & BELDING, 1957; LEBER, 1982). At the same time, WADE's (1967, 1968) conjecture that differences in diet are responsible for the variation in shell colors and markings, combined with the great difficulty of making Mendelian paired matings of bivalves, has caused students of ecological genetics to avoid the genus. Only CHANLEY (1969) has succeeded in spawning *D. variabilis* in the laboratory, and he used mass, not controlled, matings. However, evidence for the simple genetic basis of shell polymorphisms in other bivalve mollusks is becoming available (CHANLEY, 1961; INNES & HALEY, 1977; ADAMKEWICZ & CASTAGNA, 1988). It is reasonable to begin a detailed study of the polymorphism in *Donax,* using analogies to known genetic systems until attempts at genetic analysis are successful.

Three workers (SMITH, 1975; MIKKELSEN, 1978; SCHNEIDER, 1982) have examined the polymorphism under the assumption that it is genetic and might be maintained by selection. Each of the three suggests that apostatic selection (CLARKE, 1962) or reflexive selection (MOMENT, 1962) exerted by visual predators might explain the wide variety encountered. ALLEN (1988) and OWEN & WHITELEY (1988) have raised the issue again in discussing the enormous amount of variation in the genus *Donax.* However, a thorough study of the problem has not yet been undertaken. The most immediate need is for a systematic description of the variation present. When considered as unitary morphs, the shells are so varied that no two individuals appear to be alike, and this polymorphism needs to be reduced, perhaps by subdividing it into several independently varying traits. Two additional needs are a test of the stability of frequencies over time at one site and an examination of frequencies at a single time over an extensive geographic area.

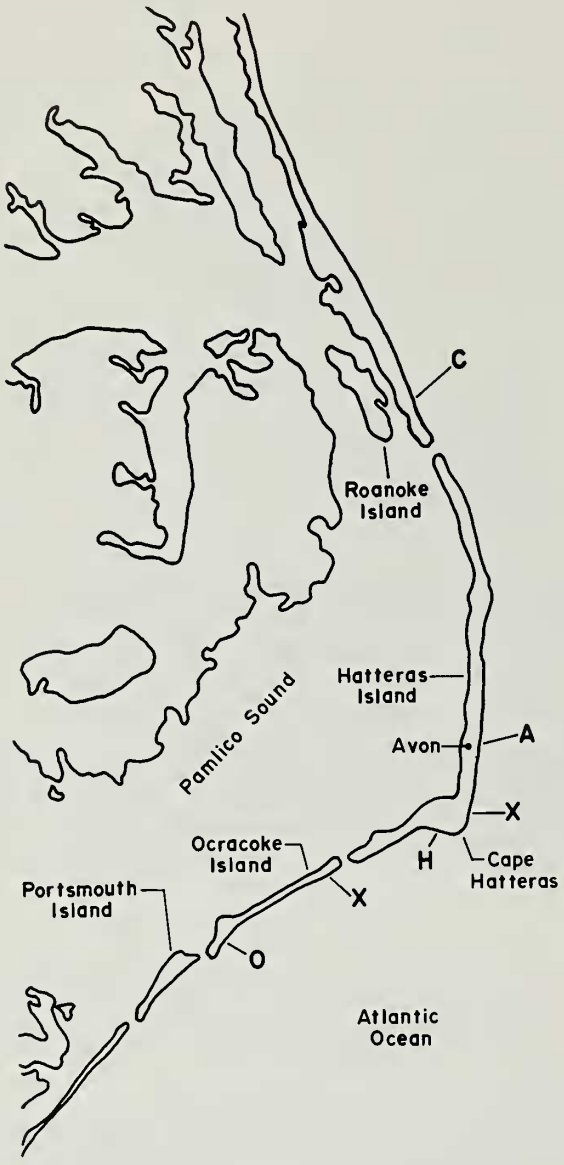

Figure 1

Map of North Carolina's outer banks showing the collection sites from north to south as follows: C = Coquina Beach, A = Avon, H = Hatteras, and O = Okracoke. At the sites marked X, no specimens of *Donax variabilis* were found.

MIKKELSEN (1978) has made a beginning on all three points with his work on *Donax variabilis* in Florida, where he followed one Atlantic and one Gulf population over a six-month period. While he reports substantial differences in shell sizes and in frequencies of various morphs between the two sites, he does not report having tested frequencies of morphs over time in either location nor does he report any data on size of shell by morph. Mikkelsen has also chosen to use an objective, quantitative measure of shell color, the Munsel Color System (KELLY & JUDD, 1955). This choice does permit an objective designation of the overall impression given by a shell, but it makes recognition of individual, subsidiary traits difficult. The quantitative standard also blurs the distinction between qualitative (perhaps genetics) and quantitative (perhaps environmental) differences. The present paper uses instead SMITH's (1975) approach of designating qualitative classes in the hope that a careful separation of the different aspects of color and pattern will serve as a guide to genetic experiments. To promote standardization of classification, the author has placed in the collection of the U.S. Museum of Natural History a set of labeled shells that exemplify the variants described here. The present study also determines both the length of the shell and the value of each character for each clam collected. When recruitment is episodic, as it is in *D. variabilis*, these data sometimes permit the detection of differential growth and (or) survival among morphs and may provide information about the agents that affect the polymorphism.

With these changes of method, the present study attempts to extend our knowledge of the polymorphism by dissecting it into several components and then examining their frequencies in samples taken at a single time across what is known to be a major biogeographical boundary. If differences in geographical location were to be correlated with changes in frequencies among morphs, this would be evidence that the polymorphism in *Donax variabilis* is maintained at least in part by environmental selective agents. Because Cape Hatteras, North Carolina, represents a dividing line both for water circulation patterns and for the northern and southern forms of many marine organisms, it is a promising location in which to examine the frequencies of shell colors and patterns. In addition, two unpublished studies suggest that Hatteras might be an area of rapid changes in frequency. The frequencies of various shell morphs differ significantly in collections from Virginia and Florida, and sharp changes in the frequencies of alleles for the gene encoding leucine aminopeptidase occur around Cape Hatteras. The purpose of this paper is to report shell lengths and the frequencies of several shell characters in samples taken around Cape Hatteras in October of 1986.

MATERIALS AND METHODS

Collections

Donax variabilis inhabits the wash zone of sandy beaches from Delaware to Florida and around the Gulf of Mexico. The species occurs sporadically but can reach a density of 15,619 per m^2 (NELSON, 1985) in some locations. For simplicity, the clams from a single site are referred to as a population, but it is not known whether the individuals at a given site are in fact an interbreeding population or whether they are simply an aggregation of individuals from more than one source (NELSON, 1985). The animals de-

scribed here were collected on 12 and 13 October of 1986 from four sites along the outer banks of North Carolina (shown in Figure 1). Of six sites visited, only four had aggregations of *Donax* and these four were sampled as described below. The sites covered a linear distance of approximately 114 km: 64 km between Coquina and Avon, 10 km between Avon and Hatteras, and 40 km between Hatteras and Okracoke. They were chosen primarily for accessibility and secondarily for regular spacing around the cape. No effort was made to quantify the characteristics of the beach sites. The four sites did differ in their slopes (with Hatteras steepest) and in the amount of broken shell present, but, by subjective judgement, the substrate colors were alike.

Each site was visited during daylight within one and one-half hours of a low tide. The wash zone was examined and, when *Donax* were sighted, the beach to a depth of about 4 cm was shoveled into a sieve and washed to remove the sand. The mesh of the sieve was 3 mm with a diagonal opening of 4.2 mm and, while the sieve retained an unknown proportion of animals below 4 mm, it clearly did not retain all of them, nor could it trap very small individuals. To obtain an unbiased sample of all sizes would require taking cores of the beach. For purposes of this study, emphasis was placed on obtaining a large sample of adult animals in a short period of time. Similarly, no attempt was made to estimate population densities. Rather, collecting effort was adjusted to produce approximately equal sample sizes. Extra effort did not achieve a sample from Avon equal to those from the other sites, indicating that the population there was indeed less dense.

Once a sample had been sieved, the retained broken shells and living clams were placed in bags with ethyl alcohol (which does not affect the shell or its colors) and transported back to the laboratory where the *Donax* were separated from the debris. Each shell was cleaned, its length was measured with calipers to the nearest 0.1 mm, and its color and pattern elements were recorded both for interior and exterior surfaces. Every animal counted had clearly been collected alive and its two valves were always kept together. The data were later analyzed with the SAS statistical package, primarily with the procedures "FREQUENCY" and "ANOVA," executed on a VAX 8800 computer at George Mason University.

Shell Characters

For their studies, Smith (1975), Mikkelsen (1978), and Schneider (1982) classified shells primarily by their overall appearance with some markings, especially rays, also noted. The present study does not use this approach. The colors and markings are distinctive enough to be treated as qualitative variables and they can be scored consistently by eye. Furthermore, the overall appearance of the shell is determined by the interaction of what appear to be several independent characters. While the names chosen for these characters might vary among investigators, the categories themselves are easy to recognize. Most of these correpond to characters recognized by Mikkelsen and these are noted where appropriate.

At least four pigments of unknown chemistry account for the colors seen in these Cape Hatteras samples of *Donax variabilis*. These colors are yellow, brown, red, and purple. A fifth color, white, is most probably the absence of any pigment. Each of these pigments is characteristic of different pattern elements on the shell. For the purposes of this study, the multiplicity of colors and patterns seen in *D. variabilis* were reduced to the following five characters:

Background. The background color of the shell can be either yellow or white (uncolored). Occasionally a shell may appear to be another color, but this effect is generally attributable to the presence of other pigments applied in one of several patterns over the background color which cause reflected colors. No third background color such as reported by Mikkelsen (1978, in Sanibel, Florida) was observed. However, in Florida *Donax* are even more colorful and variable than they are in North Carolina.

Umbo. The umbo region of the shell can be unmarked, in which case it shows the background color of the shell, or it can be covered with a spot of color, either purple or red. This character is the same as the "P-Umbo" of Mikkelsen (1978).

Rays. The shell can be marked with rays radiating from the umbo toward the growing lip. In some cases the shell has two or three purple rays that do not extend all the way to the lip. This is the P-J-R or P-juvenile pattern of Mikkelsen (1978). In other cases, the rays are red or brown rather than purple and extend from umbo to lip much like the pattern in tellinid clams. Although in the present study both of these patterns are called "rays," they are almost certainly different traits. The incomplete rays are always purple and few in number while the complete rays are never purple and are usually more than three in number.

Rings. Periods of faster and slower growth produce rings in the shell independent of any pigmentation. When pigment is secreted periodically, the shell can be marked with rings of color that run parallel to the growing lip. If the rings were either white or yellow, they were discounted as part of the normal growth process. If the rings were purple or red, the shell was counted as ringed. Brown rings were never seen. The distinction between the systems for rings and rays is demonstrated by rare shells that have both brown rays and blue rings.

Inside. The interior of the shell can be unpigmented. Conversely, it can be marked with purple pigment that covers (a) only the posterior half of the shell (toward the foot, the pattern designated "half") or (b) the entire inner surface of the shell ("entire"). One of the principal difficulties in interpreting earlier studies is the authors' omission of any mention of color inside the shell. This pigment can often be seen through the shell of the living

Table 1

Frequencies of various shell characters of *Donax variabilis* by collection site. The last column gives the probability (*P*) associated with a χ^2 test of homogeneity for the frequencies of variants for the character among the four sites.

	Collection sites				
Shell character	Coquina (n = 479)	Avon (n = 167)	Hatteras (n = 494)	Okracoke (n = 411)	*P*
Background					
Yellow	0.487	0.473	0.453	0.372	0.004
White	0.513	0.527	0.547	0.628	
Umbo					
Unmarked	0.771	0.826	0.879	0.698	0.0001
Purple	0.129	0.096	0.095	0.095	
Red	0.100	0.078	0.026	0.207	
Rays					
Absent	0.263	0.174	0.366	0.292	0.0001
P-juvenile	0.601	0.712	0.496	0.589	
Brown/red	0.136	0.114	0.138	0.119	
Rings					
Absent	0.722	0.731	0.567	0.514	0.0001
Purple/red	0.278	0.269	0.433	0.486	
Inside					
Uncolored	0.566	0.605	0.591	0.611	0.0001
Half	0.133	0.042	0.045	0.083	
Entire	0.301	0.353	0.364	0.306	

animal thus giving a bluish tint to a white animal or a muddy brown tint to a yellow one.

RESULTS

Frequencies of Shell Characters

Comparison of the four samples clearly demonstrates that aggregations of *Donax variabilis* are not uniform around Cape Hatteras, while the same comparison refutes the idea that regular north-south clines occur for most characters. Table 1 shows the frequencies by site for the variants of each shell character. When the frequencies for any one character are compared over all sites with a χ^2 test, the results show a significant deviation from homogeneity in every instance (probability always less than 0.01). Not only do the sites differ in the frequencies of these variants, the pattern of these differences among sites is not the same for all the characters. The character "background" exhibits a consistent decrease in the frequency of yellow from north to south at the same time that the characters "umbo" and "rays" show the northern and southernmost sites to be most alike. For the character "rings," the two northernmost sites form a pair in contrast to the two southernmost locations, while the character "inside" shows no obvious pattern at all. Because the frequencies of these variants change significantly over rather short distances and because that pattern of change is different for each character, each site has a distinctive suite of frequencies.

While the combination of these patterns and colors does lead to a large number of morphs, the five shell characteristics do not always occur independently of one another. Table 2 summarizes the results of pairwise χ^2 tests of independence for each possible pair of characters at each sampling site. Despite the potential for spurious significance when large numbers (40) of tests are performed, the results are clear. For any pair, either the χ^2 values had probabilities at or above the 0.05 level for all sites, in which case the pair was considered to be independent, or else the values were at or below the 0.001 level for at least three of the sites, in which case the pair was considered to be associated.

Background color of the shell is independent of markings on the shell with one exception, the presence of a colored umbo. At each site, regardless of frequencies, red umbo appears on shells with yellow background color far more often (overall frequency 0.145) than on shells with white background (overall frequency 0.067). Purple umbo (overall frequencies of 0.101 and 0.109 on yellow and white backgrounds respectively) does not show this pattern. The cause of the association is unknown, but it cannot be forced by the pigment system because it is not absolute. A shell can have either background color with either umbo color.

The presence of rays of any kind is independent of the presence of rings, and one does find shells with both brown rays and clearly developed purple rings. The other five pairs of shell markings show significant associations with

Table 2

Results for χ^2 tests of independence performed on each pair of *Donax variabilis* shell characters for each site. To compensate for the multiple testing, a significance level of alpha = 0.001 was used. If an association is marked with **, it was significant at this level in each of the four samples. A mark of * indicates significance in three of the four samples. χ^2 values for the other pairs only sporadically reached the 0.05 level of probability.

Character pair	Independent	Pattern of occurrence
Background & umbo	no**	red ubmo occurs more frequently on yellow background than on white
Background & rays	yes	random
Background & rings	yes	random
Background & inside	yes	random
Umbo & rays	no**	pigmented umbo and rays of any kind not usually present together
Umbo & rings	no**	shells with purple umbo are more likely to have blue rings
Umbo & inside	no**	shells with purple umbo usually have pigmented insides
Rays & rings	yes	random
Rays & inside	no*	no consistent pattern
Rings & inside	no**	shells with purple rings are more likely to have pigmented insides

one another and four of these associations appear to have the same basis. If any one purple marking is present, the chance that another purple mark will be present increases. In particular, when a purple umbo is present, the inside of the shell is much more likely to be either half or entirely pigmented than when the umbo is not colored. The overall frequency of shells with interior pigment is 0.411, while among shells with purple umbo it is 0.820 and among shells with unpigmented umbo it is 0.302. The one association that does not follow the pattern of one purple marking increasing the likelihood of another is that between pigmented umbo and rays. When the umbo is pigmented, rays of any kind are present less frequently (0.599) than when the umbo is pigmented (0.826). The cause of these associations is not known, but presumably the ability to produce purple pigment is a prerequisite for the expression of any pattern involving purple pigment.

Shell Characters and Length

Figure 2 shows the distribution of shell lengths at each site. Clearly, the four samples are heterogeneous for shell length just as they are for the frequencies of the shell characters. Each mean is significantly different from those

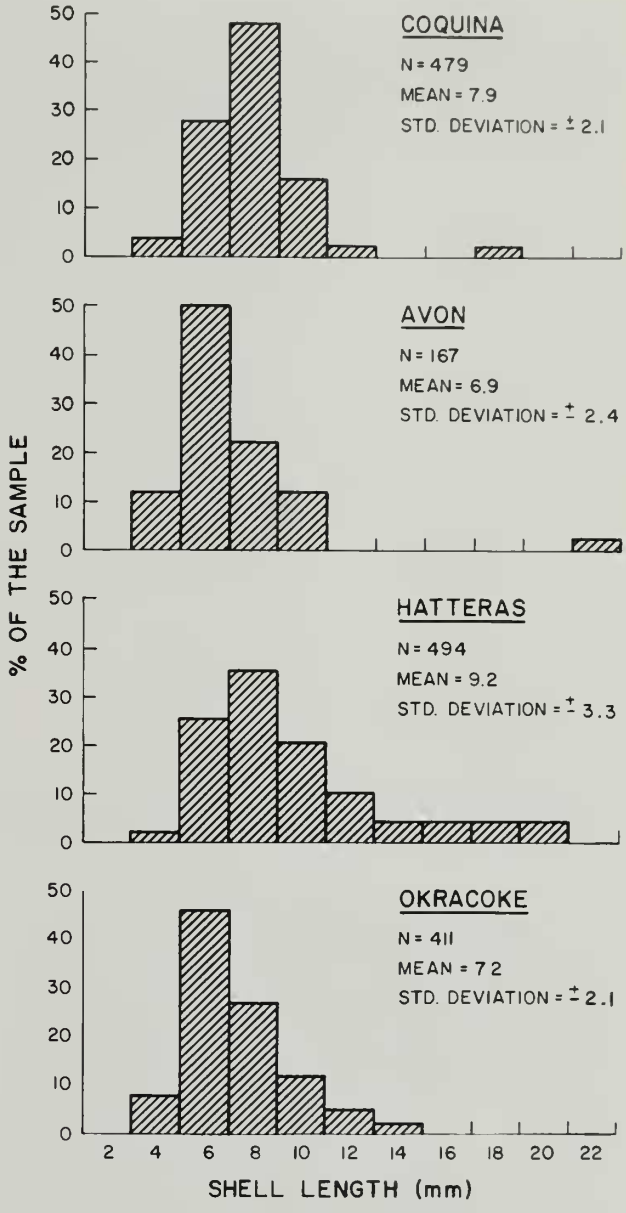

Figure 2

Distribution of shell lengths of *Donax variabilis* at the four collection sites.

at the adjacent sites (ANOVA with Duncan's Multiple-Range Test, $P < 0.05$) although the means for Avon and Okracoke do not differ significantly. The truncation of the distribution toward 2 mm shell length undoubtedly reflects the fact that the collection technique did not reliably detect smaller animals. Even with this distortion, one can see that the Hatteras sample contains a far greater proportion of larger animals than any other site and that Avon has the smallest clams.

Table 3

Mean shell length in millimeters (with standard error) for the variants of each *Donax variabilis* shell character by collection site. Asterisks signify that adjacent means for a given site are significantly different at the 0.05 level either using a two-tailed *t*-test for two means or Duncan's multiple-range test for three.

	Collection sites			
Shell character	Coquina (n = 479)	Avon (n = 167)	Hatteras (n = 494)	Okracoke (n = 411)
Background				
Yellow	8.2 (±0.15)*	7.3 (±0.27)	9.5 (±0.23)	7.4 (±0.17)
White	7.5 (±0.11)*	6.6 (±0.25)	9.0 (±0.19)	7.2 (±0.13)
Umbo				
Uncolored	7.6 (±0.11)*	6.9 (±0.21)	9.3 (±0.16)	7.3 (±0.13)
Purple	8.5 (±0.20)	5.9 (±0.33)	8.4 (±0.40)	7.6 (±0.33)
Red	8.6 (±0.21)	8.2 (±0.37)*	9.2 (±1.03)	7.0 (±0.16)
Rays				
Absent	8.2 (±0.15)	7.8 (±0.81)	9.6 (±0.28)	7.4 (±0.21)
P-juvenile	7.9 (±0.13)*	6.8 (±0.15)	9.4 (±0.23)	7.2 (±0.15)
Brown/red	7.2 (±0.22)*	6.0 (±0.35)	8.6 (±0.36)	7.0 (±0.23)
Rings				
Absent	7.6 (±0.11)*	6.7 (±0.19)*	8.7 (±0.18)*	6.7 (±0.14)*
Purple/red	8.6 (±0.17)*	7.5 (±0.43)*	9.9 (±0.24)*	7.8 (±0.15)*
Inside†				
Uncolored	7.6 (±0.13)	6.6 (±0.17)	8.9 (±0.17)	6.9 (±0.12)
Half	8.0 (±0.16)	12.1 (±2.61)*	10.4 (±1.00)	8.3 (±0.40)*
Entire	8.2 (±0.17)	6.9 (±0.21)	9.6 (±0.26)	7.6 (±0.19)

† An analysis of variance shows that the effect of inside coloration on shell length is significant at each site. In each case, the largest and smallest means differ significantly and, where marked*, adjacent means differ.

Mean lengths of the shell for the morphs of each character are given in Table 3. For each character at each site, an analysis of variance tested the hypothesis that shell length was influenced by which morph was present. The results of these ANOVAs were not always significant, and the presence or absence of a colored umbo appears to be unrelated to shell length. For inside pigmentation, background color, rays, and rings, however, one morph is consistently larger than another even though the effect is often not significant. Shells with pigmented interiors are always larger than shells with no pigment. Shells with yellow ground color are always larger than shells with white ground color (probably the absence of pigment). Shells with no rays are consistently larger than shells with the p-juvenile pattern which are in turn always larger than shells with brown rays, although the effect is significant only at the Coquina Beach site.

DISCUSSION

Unless genetic data become available, one cannot be certain of the correct interpretation for the color and pattern variants in *Donax variabilis*. However, one can argue by analogy with other molluscan systems that these variants are quite likely to have simple Mendelian bases. In the land snail *Cepaea* (Cain *et al.*, 1960), the coloration of the spire, white or pink, is determined by a single gene and this situation may well be analogous to the pigmentation of the umbo in *D. variabilis*. Three examples are available from other marine bivalves: (1) the presence of rays on the shell, a pattern very similar to brown/red rays in *D. variabilis*, is determined by a single gene with incomplete dominance in the clam *Mercenaria mercenaria* (Chanley, 1961), (2) the background shell color, white versus yellow or orange, is controlled by a single gene in the scallop *Argopecten irradians* (Adamkewicz & Castagna, 1988), and (3) the difference between purple and brown shell color in the mussel *Mytilus edulis* is also determined by a single gene (Innes & Haley, 1977). Such examples of genetic control over shell characters make it unlikely that similar phenotypes in *D. variabilis* are environmentally determined as Wade (1968) originally suggested. The significant differences in frequencies of these characters among sites probably reflect differences in gene frequencies, while the independence of the various components of the polymorphism suggests that each component may be responding to different forces. The immediate challenge is to discover why these differences exist and what the causes might be.

The heterogeneity of samples over relatively short distances is surprising, particularly in a marine organism with a planktonic larval stage, and shows a clear need for

studies over still shorter distances. All previous work has suggested that difference among sites would show broad geographic patterns. OWEN & WHITELY (1988) have noted a relationship in the genus *Donax* between amount of variation and latitude, with the more colorful species occurring in the south, and the same pattern holds within the species *D. variabilis* where populations are much more colorful in Florida than in Virginia. However, in *D. variabilis,* even background color, which does show a consistent decrease in the frequency of yellow from north to south, must be even more heterogeneous over distance than appears from the present study. MIKKELSEN (1978) reports that the proportion of yellow at Indialantic Beach on the Atlantic coast of Florida is 62%, which means that the frequency of yellow must rise substantially somewhere south of Okracoke. Red markings of any kind become more frequent as one moves south along Hatteras, but this trend appears not to continue south to Florida where red is much more common on the Gulf coast than on the Atlantic. Assuming that the basis for these differences is variation in allele frequencies along the coast, the observed heterogeneity must have one of two causes. Either the differences represent random variation in neutral traits or else they are the result of natural selection which differs in intensity, direction, or both from site to site.

Each interpretation has both advantages and difficulties. If genetic drift produced the observed frequencies, then the breeding populations of *Donax variabilis* must be much smaller and more localized than one would expect either from their observed numbers on beaches or from their mode of reproduction. Such a population structure is not impossible, but it implies that only a small fraction of the adults (perhaps unseen in offshore areas) ever reproduces successfully. If natural selection produced the observed differences in frequencies, then the beach habitat along the North Carolina coast is more heterogeneous, on a finer scale, than appears at first examination. Selection by water temperature and (or) salinity, factors that vary on a large scale, should produce regular clines, not the heterogeneous patterns observed. The visual predators observed by SMITH (1975) and SCHNEIDER (1982) have large foraging ranges and do not vary in population density over such short distances. If crypsis and visual predation are involved, then the beaches must differ more in color and (or) composition than is apparent by casual examination. SMITH (1975) proposes that young *Donax* resemble individual grains of sand and that one must examine a beach on that scale in order to detect crypsis. His suggestion that the frequencies of different colors among the grains of sand on a beach influence crypsis should be investigated further. A final possibility, related to Smith's proposal, is that selection is apostatic, or negatively frequency dependent (CLARKE, 1962; MOMENT, 1962). If a morph's fitness depends on its frequency, then clams in all of the samples might be responding to the same forces while populations were in different stages of a complex and shifting equilibrium.

Understanding the cause of heterogeneity in shell lengths will be a key to understanding the forces acting on the polymorphism. Because the ages of these clams are unknown, the data cannot distinguish between the effects of growth rate and age on length of the shell. However, the life cycle of *Donax variabilis* in only one year long (NELSON, 1985) and shell length reflects at least approximate age. Three possibilities exist. (1) The clams in any given sample may indeed be members of a single, transient breeding population. Differences in sizes among sites would be the result of foundings at different times. This model is consistent with the observation that *Donax* occurs sporadically on many beaches. (2) The clams at any one site might, as MIKKELSEN (1985) believes possible, be a mixture of individuals washed in from several different breeding populations. (3) The heterogeneity of shell lengths might result from different growing conditions at each site. In this view, animals that began growth at the same time would reach larger sizes in areas that had superior conditions. WADE (1967, 1968) has proposed this explanation for the substantial size differences he found on different beaches.

Any of the three interpretations leads to the conclusion that *Donax variabilis* is highly subdivided, and the models differ only in whether the animals in one sample are regarded as members of a breeding population. The evidence is insufficient but favors either the first or third interpretation. An examination of the shell lengths at each site shows a unimodal distribution typical of a single population of mixed ages. It seems unlikely that a mixture of animals from several sources would produce the same distribution. The distinction is a critical one for study of the polymorphism because, if the mixture model should prove to be correct, frequencies of morphs in any one sample would be meaningless and the polymorphism could not be understood until the source populations were located and studied. If the varying growth rate model is correct, then selection based on resource availability becomes more probable, while if the isolated population model is correct, drift based on founder effects becomes more likely. Clearly, any future studies must be conducted with fine scale sampling and attention to demographic parameters.

The data on mean shell length for each character do show that heterogeneity of shell lengths among sites cannot itself be the cause of heterogeneity in the frequencies of the shell characters. For shell length to influence morph frequency, size would have to affect either the ability of the clam to form the character or the ability of the investigator to detect it. The data do not support either possibility. Background color of the shell does not change during the life of an individual and the smallest clams can be recognized as either white or yellow. Furthermore, the highest and lowest frequencies of yellow do not occur at the two sites most different in mean length. Similarly, the colored umbo is equally distinct at all shell sizes and its frequency at a site is unrelated to mean shell length at that site. The rayed patterns are actually more difficult to see on small shells and, if the appearance or detection of rays were causally related to shell size, one would expect

the mean size to be larger for rayed shells than for unrayed. In fact, the reverse is true. The relationship between shell length and the presence of rings also might depend on shell length, with individuals required to reach a certain size before secreting the first ring. However, the data do not support even this hypothesis because the frequency of rings is highest in the sample (Okracoke) with the second smallest mean length.

The most interesting associations with shell length are those of background color and inside pigmentation. Not only is the mean for yellow shells always larger than the mean for white, but the presence of pigment inside the shell always yields shells with a larger mean than does absence of pigment. Oddly, the shells with only half the inside covered with pigment have a larger mean than those that are fully colored. It is possible either that darker shells grow faster, perhaps by absorbing more heat, or that darker shells survive better. The present data will not distinguish between differences in survival and differences in growth rate, but MITTON (1977) has shown a definite association between shell color and survival at high temperatures in the mussel *Mytilus edulis*. To distinguish between the possibilities, any future study must follow frequencies over time at a single site.

In summary, the data show that aggregations of *Donax variabilis* are highly heterogeneous over relatively short distances both for shell length and for the frequencies of five polymorphic traits. Each site presented a unique combination of shell lengths and morph frequencies and neither mean shell length nor the frequencies of any of the five characters showed a consistent pattern of change among the five sites. The variations in frequency of the shell characters do not show a common pattern and the variations in size and in frequency cannot be causally related. Most probably, *Donax variabilis* in the Hatteras region forms disjunct populations that initiate at different times and (or) respond to extremely local environmental conditions. Any future studies must examine differences in *Donax* over very short distances preferably over at least a year's time.

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